

INFLUENCE OF TEMPERATURE AND PHOTOPERIOD ON  
EARLY DEVELOPMENTAL RATE OF  
*TENODERA SINENSIS* SAUSSURE (MANTODEA: MANTIDAE)

L. E. HURD, P. E. MARINARI, AND R. M. EISENBERG

Ecology Program, School of Life Sciences, University of Delaware, Newark, Delaware 19716.

---

*Abstract.* — Rate of development for the first two instars of the mantid *Tenodera sinensis* (Saussure) increased with increasing temperature for cohorts maintained at 20°C, 25°C and 32°C. An increase in incubation temperature from 20°C to 32°C decreased time in instar by more than two thirds for photoperiods of 8L:16D, 16L:8D and 24L:0D. The effect of photoperiod was less pronounced, partly because immobile mantid nymphs could feed in the dark when nocturnally active prey came into contact with them. Total prey consumed and biomass of nymphs at ecdysis did not differ among treatment groups. The effect of temperature apparently was to increase feeding rate, thereby decreasing the time required to consume the threshold amount of prey biomass necessary to trigger molting.

*Key Words:* Mantodea, Mantidae, *Tenodera sinensis*, development, temperature, photoperiod, predators

---

As with other univoltine insects inhabiting temperate regions, the life cycle of the mantid *Tenodera sinensis* (Saussure) is constrained by seasonality: it must emerge early enough in the spring to complete its life cycle before the onset of freezing temperatures in the fall, yet not so early that it is in danger of late spring frosts. In addition to these abiotic limits, prey are scarce early in the spring and late in the summer and fall, so that food limitation effectively narrows the temporal window available for success in terms of survival and fecundity (Eisenberg et al. 1981, Hurd and Eisenberg 1984).

There are three potential disadvantages to emergence early in the spring: 1) prey are scarcer than later in the spring, 2) temperatures are cooler and the risk of freezing from a late frost is significant, and 3) photoperiods are shorter. Food shortages for first instar *T. sinensis* nymphs, decrease survivorship and retard development (Hurd

and Eisenberg 1984, Hurd and Rathet 1986). The importance of temperature to insect development in general has been well-documented (e.g. Tauber et al. 1986, Bowler and Cossins 1987), which led us to ask how important this abiotic factor may be to growth rate of *T. sinensis*. Photoperiod, which increases less dramatically than temperature from early to late spring, might also be important to visual predators such as mantids because it presumably determines the amount of time available for prey capture. Here we ask how temperature and photoperiod affect developmental rate in newly hatched nymphs of *T. sinensis*.

#### MATERIALS AND METHODS

Oothecae of *T. sinensis* were collected from New Castle County, Delaware, during the winter of 1988 and kept in the laboratory at 10°C. These oothecae were subsequently incubated at 25°C to induce hatch-

ing. Upon hatching, nymphs were divided among three treatment groups of 30 nymphs each, which differed in hours of light vs. dark per day: 8L:16D, 12L:12D, and 24L:0D. The entire light:dark series was run at three temperatures with three separate cohorts: 20°C, 25°C, and 32°C. The broad range of light and temperature was chosen to provide the greatest opportunity for these abiotic factors to influence development. Five additional nymphs were kept in total darkness at 25°C and otherwise treated as above, to serve as a check on whether any feeding could take place in the dark.

Nymphs were housed individually in 130 ml glass vials fitted with plastic lids, which were ventilated with fine mesh brass screen. Cotton-tipped swabs were inserted through holes in the caps and the tips were wetted daily with distilled water. Mantid nymphs were allowed to crawl into the vials upon hatching, and were not handled thereafter in order to avoid injury. All mantid nymphs were provided prey *ad libitum*, in the form of apterous *Drosophila melanogaster* (Meigen). Numbers of flies consumed in whole or in part were recorded, and all flies were replaced daily.

The first 10 nymphs in each group to molt were killed by freezing, measured for body length (top of head to tip of abdomen), dried at 60°C for 48 h and weighed. This experiment was carried out for the first two stadia.

Data obtained in this experiment generally did not meet the homogeneity of variance criterion necessary for the application of parametric ANOVA. Therefore the effects of photoperiod and temperature were analyzed using nonparametric Kruskal-Wallis tests (Sokal and Rohlf 1981).

## RESULTS

Temperature had the most pronounced effect on developmental rates for both instars. Examination of the pattern of molting among experimental cohorts revealed a consistent decline in stadium length with

increasing temperature for all three photoperiods (Table 1).

The effect of photoperiod was both less dramatic and less consistent. Photoperiod was not correlated with developmental rate within temperature groupings for first instars (Table 1). The only significant difference within a temperature group was a slightly greater mean stadium length in nymphs exposed to 16 hours of light at 25°C. Photoperiod had a greater effect on developmental rate of second instars than firsts. Stadium duration declined significantly between the 8L:16D and 16L:8D groups for nymphs incubated at 20°C and 32°C, but not at 25°C (Table 1).

Feeding rates of nymphs during both stadia were also more consistently related to temperature than to photoperiod. During first stadium, feeding rate increased with increasing temperature for all photoperiods (Table 2), but was not affected by photoperiod. During second stadium, feeding rate also increased significantly with increasing temperature for all photoperiods (Table 2). As with developmental rate (Table 1), feeding rate increased significantly between the 8L:16D and 16L:8D groups of nymphs exposed to 20°C and 32°C, but not 25°C.

Total flies consumed was not related either to temperature or to photoperiod. Mean number of flies eaten by first instars ranged from 19–22 among the nine experimental groups; for second instars the range was 35–44 flies. There was also no significant difference in biomass attained by nymphs among the various treatment groups. During first stadium, mean nymph biomass ranged from 2.2–2.9 mg; during second stadium the range was 5.3–6.1 mg.

The five first instar nymphs kept in total darkness (0L:24D) were able to feed and to complete the instar. In fact there was no significant difference between these nymphs and those kept at 24L:0D, either in rate of maturation or in feeding rate. Observations of nymphs made in the dark under red light indicated that these flies were active in the

Table 1. Mean stadium length in days ( $\pm$ SE) for *T. sinensis* nymphs. N = 10 in each cell. Asterisks indicate  $P < 0.001$  (Kruskal-Wallis test) for differences within rows and columns.

		Temperature ( $^{\circ}$ C)		
		20	25	32
First instar:				
Light : dark regime	8L:16D	16.7 (0.21)	8.9 (0.10)	5.4 (0.16)*
	16L:8D	17.3 (0.49)	9.4 (0.16)	5.0 (0.00)*
	24L:0D	16.9 (0.10)	8.0 (0.00)	5.0 (0.00)*
		ns	*	ns
Second instar:				
Light : dark regime	8L:16D	27.2 (0.66)	9.4 (0.24)	6.4 (0.40)*
	16L:8D	15.6 (0.60)	9.4 (0.51)	5.0 (0.31)*
	24L:0D	16.2 (0.49)	9.4 (0.24)	5.0 (0.00)*
		*	ns	*

dark, and were captured by stationary mantid nymphs when contact was made. Therefore, *T. sinensis* nymphs are at least capable of night feeding by tactile cues, even when they cannot see prey. This, of course, does not explain the significant effects of photoperiod on second instar nymphs (see above).

DISCUSSION

Our results suggest that temperature is more important than photoperiod to developmental rates of the first two instars of *T. sinensis*. The initial assumption that photoperiod places a limit on time for prey capture was found to be incorrect, at least dur-

ing first stadium. However, we do not know to what extent night feeding is a useful adaptation, or simply a laboratory artifact of confining nymphs to vials in which nocturnally active prey are abundant. Some ambush predators, such as thomisid spiders which use flowers as feeding sites, routinely feed at night as well as during the day (Morse 1981, R. Fritz pers. comm.). However, mantid nymphs are not flower specialists, which calls into question how often prey are likely to blunder into them in the dark in the absence of such an attractant.

Although temperature has been found to have profound effects on body size and even adult fecundity in other insects (e.g. Laugh-

Table 2. Mean ( $\pm$ SE) feeding rates of mantid nymphs fed *ad libitum*, in terms of number of flies consumed/nymph/day. Asterisks indicate  $P < 0.001$  (Kruskal-Wallis test) for differences within rows and columns.

		Temperature ( $^{\circ}$ C)		
		20	25	32
First instar:				
Light : dark regime	8L:16D	1.34 (0.34)	2.08 (0.09)	3.58 (0.14)*
	16L:8D	1.32 (0.05)	1.92 (0.09)	4.43 (0.11)*
	24L:0D	1.34 (0.08)	2.27 (0.09)	3.85 (0.11)*
		ns	ns	ns
Second instar:				
Light : dark regime	8L:16D	1.73 (0.08)	4.87 (0.04)	5.49 (0.56)*
	16L:8D	2.88 (0.16)	3.74 (0.45)	8.16 (0.43)*
	24L:0D	2.79 (0.14)	4.81 (0.37)	8.80 (0.34)*
		*	ns	*

lin 1964), there was no relationship between temperature and size at ecdysis for first and second instar *T. sinensis*. Additionally, there was no relationship between temperature and total prey consumed. Feeding rate, however, consistently increased with increasing temperature. Therefore, the effect of increasing temperature was to decrease the time necessary to consume a threshold amount of prey biomass in order to trigger molting.

These results raise a question about the life history strategy of this species: Why does egg hatch occur so early, at a risk of starvation and late frost, when hatching a few weeks later would expose them to increased temperature and prey density, both of which facilitate faster development? For instance, 20°C and 25°C correspond roughly to daytime temperatures during late April and late May, respectively, in our area (Bair and Ruffner 1985). This five degree increment resulted in a 43% decrease (from 33 to 19 days) in the time it took to complete both first and second stadia among mantid nymphs fed *ad libitum* in our experiment (16L:8D). Nymphs which have hatched at the end of April in the field have taken up to 45% longer to develop through second instar than in this experiment (Rathet and Hurd 1983, Hurd and Eisenberg 1984), but field conditions entail variable temperatures as well as food limitation.

If abiotic advantages *per se* do not entirely account for early hatching in this species, what biotic factor(s) might be responsible? Possibilities include avoidance of predators (or parasites), and reduction in competition. Other mantid species, sympatric with *T. sinensis* here and abroad, hatch later in the spring (Rathet and Hurd 1983, Hurd 1988). These differences in egg phenology could mitigate interspecific competition by reducing size overlap among these species (Hurd and Eisenberg 1989); mantids of different sizes take different sized prey (Bartley 1983). Furthermore, larger mantids have a greater

total range of prey sizes they can effectively take than smaller ones (Bartley 1983). However, a disparity in size can also result in predation of later hatching (smaller) nymphs by those emerging earlier (Hurd 1988). Therefore, early hatching may confer an advantage to *T. sinensis* over other sympatric mantid species, which offsets the apparent abiotic disadvantages.

#### ACKNOWLEDGMENTS

This work was supported by a NSF Grant BSR 8506181. This is contribution #122 from the Ecology Program, University of Delaware.

#### LITERATURE CITED

- Bair, F. E. and J. A. Ruffner. 1985. Weather of U.S. Cities. Vol. 1. Gale Research Publishing Co., New York.
- Bartley, J. A. 1983. Prey selection and capture by the Chinese mantid. Ph.D. Dissertation, Univ. Delaware, Newark.
- Bowler, K. and A. R. Cossins. 1987. Temperature Biology of Animals. Chapman and Hall, New York.
- Eisenberg, R. M., L. E. Hurd, and J. A. Bartley. 1981. Ecological consequences of food limitation for adult mantids (*Tenodera sinensis* Saussure). *Am. Midl. Nat.* 106: 209-218.
- Hurd, L. E. 1988. Consequences of divergent egg phenology to predation and coexistence in two sympatric, congeneric mantids (Orthoptera: Mantidae). *Oecologia* 76: 549-552.
- Hurd, L. E. and R. M. Eisenberg. 1984. Experimental density manipulations of the predator *Tenodera sinensis* (Orthoptera: Mantidae) in an old-field community. I. Mortality, development and dispersal of juvenile mantids. *J. Anim. Ecol.* 53: 269-281.
- . 1989. The temporal distribution of hatching times in three sympatric mantids (Mantodea: Mantidae) with implications for niche separation and coexistence. *Proc. Entomol. Soc. Wash.* 91: 55-58.
- Hurd, L. E. and I. H. Rathet. 1986. Functional response and success in juvenile mantids. *Ecology* 67: 163-167.
- Laughlin, R. 1964. Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). VIII: Temperature and larval growth. *Bull. Ent. Res.* 54: 745-759.

- Morse, D. H. 1981. Prey capture by the crab spider *Misuma vatia* (Clerck) (Thomisidae) on three common native flowers. *Am. Midl. Nat.* 105: 358-367.
- Rathet, I. H. and L. E. Hurd. 1983. Ecological relationships among three co-occurring mantids, *Tenodera sinensis* (Saussure), *T. angustipennis* (S.), and *Mantis religiosa* (L.). *Am. Midl. Nat.* 110: 240-248.
- Sokal, R. R. and F. K. Rohlf. 1981. *Biometry*. W. H. Freeman, New York.
- Tauber, M. J., C. A. Tauber, and S. Masaki. 1986. *Seasonal adaptations of insects*. Oxford Univ. Press, New York.